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PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING PART 14. THE ARTIODACTYLS

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ABSTRACT

All artiodactyl material from the late Eocene faunas occurring along Badwater Creek in the northeastern part of the Wind River Basin, Wyoming, is described. Two indeterminate dichobunids are present together with a third form, *Apriculus praeteritus*. One indeterminate leptocoerid, two agriocoerids, *Diplobunops* and *Protoreodon*, the omomyrid *Malaquiferus*, four protoceratids, *Leptotragulus*, *Leptoreodon* and two species of *Poabromylus*, and a new genus of leptomyrid, *Hendryomyx*, are described. Correlation is made with faunas in Texas, Utah, and California and the paleoenvironmental conditions are discussed. Relationships of the late Eocene selenodont artiodactyls are reviewed.

INTRODUCTION

Knowledge of late Eocene artiodactyls has been enhanced greatly in recent years through the work of Wilson (1971, 1974) and Golz (1976). Prior to these reports, Gazin's paper (1955) stood as the only major recent summary and his review of the dichobunids in that paper is still the only comprehensive study of that group for the late Eocene. As a result of their studies, the presence of the Hypertragulidae, Agriocoeridae, and Protoceratidae has been extended back into the late Eocene. Camelids are also present at that time but are only poorly represented and understood. The transition from basically low crowned bunodont forms to the higher crowned varieties of selenodont artiodactyls is a late Eocene event. By the beginning of the Oligocene

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Table 1.—*Artiodactyls in the Badwater faunas.*

Locality	Taxa
	Family Dichobunidae
5, 7	Dichobunids indet. (2 genera)
7	<i>Apriculus praeteritus</i>
	Family Leptochoeridae
Wood	Leptochoerid indet.
	Family Agriochoceridae
5, 6	<i>Protoreodon</i> cf. <i>P. petersoni</i>
5, 6, 20 and Wood	<i>Diplobunops matthewi</i>
	Family Oromerycidae
5, 6, 7	<i>Malaquiferus tourteloti</i>
	Family Protoceratidae
5, 6, 20 and Dry Fork	<i>Leptotragulus medius</i>
5, 6, 7	<i>Leptoreodon</i> sp.
20	<i>Poabromylus golzi</i> new species
7	<i>Poabromylus</i> cf. <i>P. golzi</i>
	Family Leptomerycidae
20	<i>Hendryomeryx wilsoni</i> new genus and species
Wood and Rodent	<i>Hendryomeryx</i> cf. <i>H. wilsoni</i>

the only bunodont forms, which are present, are the leptochoerids together with entelodonts and the newly evolved bunodont tayassuids.

Although the selenodont groups are present and radiating by the end of the Eocene, we still know little more about their origins than was known at the time of Gazin's (1955) review. In order to document the transition Dichobunidae to Agriochoceridae, Protoceratidae, Oromerycidae, Camelidae, and Hypertragulidae, we must know a great deal more about Bridgerian dichobunids, particularly forms from environments different from those at present represented in our collections (Black, 1968).

Artiodactyls are quite diverse in the Badwater fauna with thirteen species representing ten or eleven different genera and six families (Table 1). However, only the agriochocerids, the oromerycids, and one of the protoceratids are at all abundant. Gazin (1956) in the original work on the Badwater assemblage recorded seven genera, four of them known from only a single specimen. He also recognized three species of *Protoreodon* and one of *Diplobunops*. Although the new material described below consists for the most part of isolated teeth, there are a number of jaws and maxillae of many of the species and additional skull material of *Diplobunops*. There are, however, no unquestionable associations of upper and lower dentitions except for *Diplobunops*.

Artiodactyls are most abundant at localities 5 and 6, but this is probably more a sampling bias than a true reflection of occurrence. Quarries were opened at these localities in 1966 and 1967, whereas specimens from locality 7 and the Wood locality were collected through surface prospecting and washing operations. Some quarrying was also carried out at locality 20 with two rather complete maxillae and several jaw fragments recovered.

The three most abundant and widespread species are *Diplobunops matthewi*, *Malaquiferus tourtelotii*, and *Leptotragulus medius*. *Leptotragulus medius* is also found at Dry Fork about 20 mi to the east of the Badwater localities. Dichobunids, the oromerycid, *Leptoreodon*, and *Protoreodon* cf. *P. petersoni* are found only at localities 5, 6, and 7, localities, which are considered to be somewhat older than locality 20 and the Wood and Rodent locality. Locality 20 has yielded the type material of the new leptomerycid, *Hendryomeryx*, and this genus is only known from locality 20 and the Wood and Rodent localities. A new protoceratid is also found at locality 20 with possibly one tooth of this form from locality 7.

In general there is a greater diversity of artiodactyls in the earlier levels and the more primitive bunodont species occur only in these levels. The partially selenodont oromerycid, *Malaquiferus tourtelotii*, is confined to the earlier faunal horizon. Only selenodont forms are represented in the upper faunal level with a concomitant drop in artiodactyl diversity in these levels.

All measurements are given in millimeters. Abbreviations are as follows: CM, Carnegie Museum of Natural History; USNM, National Museum of Natural History; a-p, anteroposterior; tr, transverse; N, number; M, mean; OR, observed range; SD, standard deviation; CV, coefficient of variation; m.y., million years.

I would like to thank Mary Dawson, Malcolm McKenna, Beryl Taylor, Kris Krishalka, Jack Wilson, and David Golz for their helpful comments on the manuscript.

RELATIONSHIPS OF LATE EOCENE SELENODONT ARTIODACTYLS

Relationships of the late Eocene and early Oligocene selenodont artiodactyls of North America are shown in Fig. 1. The ancestral suite of characters included separate metapodials, separate radius and ulna, selenodont but brachyodont dentition with an enlarged metaconule and transverse molars. Small protoconules and mesostyles on the upper molars, the metaconule in the hypocone position and paracone and metacone ribs are shared derived characters for this group. From this ancestral condition one group arose which initially squared up the upper molar dentition and had the lower first premolar and canine of equal size. This protocamelid gave rise to two groups—the Oromerycidae and the Camelidae. The latter evolved elongate limbs with fused

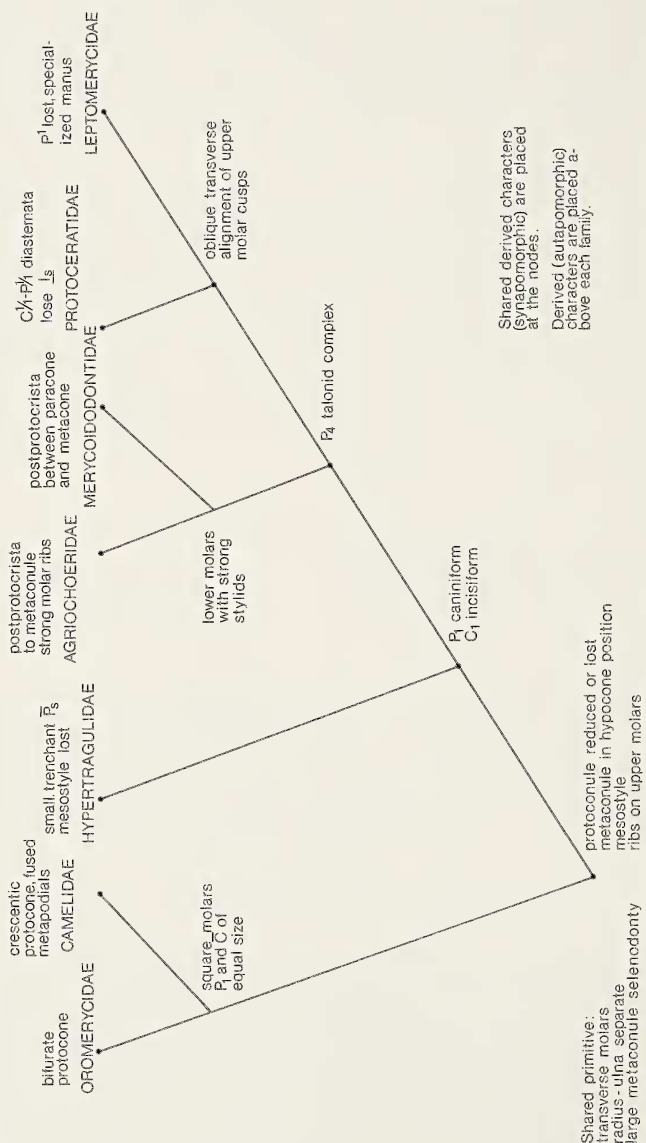


Fig. 1.—Diagrammatic representation of relationships of North American late Eocene selenodont artiodactyl groups.

metapodials and transversely compressed molars while the oromerycids maintained shorter, less reduced limbs and square upper molars. The protocone in the oromerycids became bifurcated while that in camelids became crescentic.

From the ancestral stock the remaining selenodont forms developed an incisiform lower canine and a caniniform P_1 . With loss of the upper incisors, the mesostyle and the evolution of small trenchant lower premolars the Hypertragulidae emerged. All other late Eocene selenodont groups developed a P_4 with a complex talonid and expanded the upper molars transversely. The Agriochoeridae and Merycoidodontidae evolved strong lower molar stylids with the agriochoerids emphasizing ribs on the upper molars and directing the posterior crest of the protocone towards the protoconule while the merycoidodonts developed only weak upper molar ribs or had none at all and directed the posterior crest of the protocone between the paracone and metacone.

The remaining selenodont groups known from the late Eocene evolved obliquely oriented upper molars with the protocone and metaconule positioned anterior to the paracone and metacone. One family, the Protoceratidae, evolved diastemata between the canines and P^1_1 and between P^1_1 and P^2_2 . This group also lost the upper incisors and fused the ulna and radius. The other family, the Leptomerycidae, evolved a specialized manus with reduction in carpals and lost P^1 . Of all the late Eocene selenodonts the leptomerycids appear to be the most highly specialized both in dentition and in limb structure.

I have refrained from arranging these late Eocene families in any classificatory scheme as a number of workers are reviewing particular families. However, I believe the relationships proposed in Fig. 1 to be reasonably valid.

PALEOENVIRONMENTS

The diversity and distribution of artiodactyl species at Badwater reflects not only a temporal sequence in the faunas but also a climatic change. Genera and species from localities 5, 6, and 7 occur earlier in time than do those at locality 20 and most probably the Wood and Rodent localities, and they also reflect a different environmental situation.

Selenodont species predominate throughout the Badwater sequence, but they are found together with a variety of bunodont forms in the lower faunal level, whereas no dichobunid species are known from the later localities and only one bunodont form, the earliest known leptochorid, occurs in the upper level. Although three different dichobunids are present at Badwater, they are all represented by single individuals and are not as abundant as they are in the Uinta Basin. This suggests that early in the Badwater scenario there were areas,

Table 2.—Diversity of late Eocene artiodactyls (based upon Utah, Gazin, 1955; California, Golz, 1976; Texas, Wilson, 1971, 1974; Wyoming, this paper). Bunodont genera and species are considered to be those in the families Dichobunidae and Leptochoeridae while the Agrichoeridae, Leptomerycidae, Protoceratidae, Oromerycidae, and Camelidae are considered to be selenodont groups.

Age and region	Number of genera		Number of species	
	bunodont	selenodont	bunodont	selenodont
Early Chadronian				
Texas (Porvenir)	0	7	0	8
Duchesnean				
California (Pearson Ranch)	0	5	0	5
Utah (LaPoint)	0	3	0	4
Uinta C and Randlett				
California	1	4	1	10 ¹
Utah	4	6	4	14 ²
Texas	0	3	0	4 ³
Badwater 5, 6, 7	3	6	3	6
20 and Wood	1	5	1	5
Uinta B				
California	0	4	0	5
Utah	4	6	6	8 ⁴

¹ Four species of *Protylopus* and 4 species of *Leptoreodon*.

² Seven species of agrichoerids.

³ No oromerycids of dichobunids.

⁴ Six species of dichobunids.

probably along the stream banks, where the vegetation was dense and of a tropical nature, much as in the Uinta Basin but that this type of habitat was restricted. Dichobunid dentitions would seem to be adapted for browsing on plant material less abrasive than that eaten by artiodactyls with a selenodont type of dentition. The dichobunid dentition is one that functions more to crush and pulp than to cut and grind.

At Badwater there are a variety of selenodont species, at first with the dichobunids and later by themselves. Some of the later species, particularly *Leptotragulus medius*, *Hendryomeryx wilsoni*, and *Poa-bromylus golzi*, are probably the most advanced late Eocene selenodont artiodactyls yet known.

The occurrence of these species and the diversity of the selenodont forms indicates the presence of a diversity of more abrasive food resources, perhaps even the presence of more open savanna woodland in areas away from the stream borders and perhaps higher on the mountain slopes. Webb (1977) suggests that the appearance of selenodont artiodactyls heralds the appearance for the first time in North America of a more open savanna or savanna woodland environment.

He notes that paleobotanical evidence supports the thesis that savanna woodland was developed on the lower slopes of the Rocky Mountains by late Eocene time and that it was maintained there by the dry winter seasons. He also notes the presence of grasses as indicated by pollen as a part of this savanna complex. Webb suggests that the late Eocene and early Oligocene savanna woodland in the Rocky Mountains resembled that occurring today in the Chihuahuan regions of Mexico.

Perhaps the development of savanna woodland occurred first on the Rocky Mountain slopes in response to greater seasonal temperature fluctuations than were to be found in the coastal regions of California or to the south in Texas. There is certainly a greater diversity of selenodont artiodactyl types at Badwater than have been found either in California or Texas at a comparable time (Table 2).

It is toward the end of the Eocene that filling of the intermontaine basins had progressed to the point where only the higher cores of the mountain ranges were left above the surrounding plains surface. This topographic change was undoubtedly accompanied by a floristic change with a variety of new herbs, shrubs, and trees on the landscape, perhaps similar to what MacGinitie (1953:58-59) referred to for the early Oligocene of the central Colorado Rocky Mountains as "sub-humid grassy shrub probably similar to the thorn bush and the mesquite grass formation of southwest Texas with more mesic vegetation in wide flood plains." There was certainly a variety of hardier, more drought-resistant plants on the scene in the late Eocene than had been present earlier in the Eocene. The new vegetation provided new food resources for the artiodactyls and the first suggestion of these new artiodactyl assemblages is seen in the Badwater faunas.

Webb (1977) is of the opinion that most of these new selenodont artiodactyl types were immigrant from Asia in the late Eocene. He lists camelids, hypertragulids, leptomerycids, and agriochoerids as definite immigrants from Asia, with the oromerycids, protoceratids, and merycoidodontids as possible immigrants. It is true that we are unable to trace the origins of these families into middle Eocene artiodactyl groups. However, Radinsky (1965, 1969) has demonstrated that Asia, during the late Eocene, was the center of perissodactyl radiation for both tapiroids and rhinocerotoids, and that very few artiodactyls were present in the late Eocene faunas of Asia. Therefore, most of the late Eocene selenodont artiodactyls found in North America could well be of New World origin evolving higher on the Rocky Mountain slopes or perhaps at more northern latitudes.

FAUNAL CORRELATION

Because of the varieties of different habitats sampled in California, Utah, Texas, and Wyoming, precise correlation of the faunas from

these regions is difficult. The lack of radiometric dates for most of the faunas also exacerbates this problem. There are no radiometric dates known for most of the classic Eocene sequence in the Uinta Basin of Utah and only one date of 39.3 m.y. published for the contact of the Halfway and LaPoint members of the Duchesne River Formation (McDowell et al., 1973). No K-Ar dates have been published for the late Eocene sequence in California, whereas a series of three dates bracket the Candelaria fauna in West Texas. The earliest, 40.2 ± 2.9 m.y., comes from below the fauna, whereas a date of 38.6 ± 1.2 m.y. comes from the Buckshot Ignimbrite, which overlies the fauna (Wilson et al., 1968). One date of 41.2 ± 1.4 m.y. is known for the Badwater sequence (Black, 1969) associated with the fauna from locality 20.

All of the dates known at present are associated with faunas of latest Uintan or Duchesnean aspect with no potassium-argon dates available for the classic faunas from most of Uinta time. Recent, as yet unpublished, work in the northwestern corner of the Wind River Basin and in the Washakie Basin will change this picture considerably. One other earlier date from Badwater of 45.0 m.y. (Evernden et al., 1964) is not associated with an identifiable fauna.

Some correlations can be made based on the occurrence and stage of development of the various artiodactyl species. No dichobunids are known for any of the faunas after Uinta C time, with only selenodont species occurring at locality 20, and in the Candelaria, LaPoint, and Pearson Ranch faunas (Table 2). Earlier, during Uinta C time, dichobunids are common in Utah and occur, but are scarce, in California and at Badwater. The difference in abundance and diversity during this time is, as has already been discussed, a reflection of differing habitats in the three regions. Agriochocerids and leptotraguline protoceratids occur in all four regions with the greatest agriochocerid diversity found in the Uinta Basin. *Diplobunops* is restricted to the intermontaine region, whereas *Protoreodon* is found in all late Eocene faunas.

Oromerycids are diverse in the Uinta C assemblages in California with four or five species of *Protylopus* present. In the interior only one species of oromerycid, *Protylopus annectens*, is present in the Myton fauna and the distinctive genus *Malaquiferus* in the Badwater Uinta C fauna. No oromerycids are present in the later Badwater fauna or in Texas until Oligocene time.

The earliest leptomerycid, *Hendryomeryx*, is known only from the younger Badwater faunas and from the early Oligocene Porvenir fauna of Texas. Camelids are known in California and in Utah, although sparsely represented, but are not found at Badwater or in Texas. Finally, the more advanced protoceratid, *Poabromylus*, is known only

from the LaPoint fauna in Utah, from Badwater, and from the Candelaria and Porvenir faunas in Texas.

Badwater localities 5, 6, and 7 correlate best with the Myton fauna of Utah and the Tapo Ranch, Laguna Riviera faunas of California. The Badwater locality 20 fauna is younger than the above but older than the LaPoint and Candelaria faunas and somewhat older than the Pearson Ranch fauna. The advanced aspect of some of the artiodactyls found at locality 20 is most probably due to their occurrence in a dry, more open, and perhaps more upland, situation.

SYSTEMATIC REVIEW

Order ARTIODACTYLA Owen, 1848

Family DICHOBUNIDAE Gill, 1872

Dichobunids are uncommon in the Badwater faunas with probably only three species represented, one from locality 5 and two from locality 7. Dichobunids are not common elements of any of the late Eocene faunas, but they are much more diverse in the Uinta Basin sequence than anywhere else in North America during this interval.

In California only a single dichobunid is known, *Tapochoerus egressus* from Tapo Ranch. No dichobunids are known from the late Eocene of Montana, nor from the Texas late Eocene faunas, but *Pentacemylus* is known in both places in the early Oligocene. In the Uinta Basin at least 11 species representing seven genera of dichobunids are present during Uinta B and C time, but no dichobunids persist above the Randlett horizon. The number and diversity of dichobunids in the Washakie Basin late Eocene is difficult to determine; these faunas are under study by William Turnbull. No new material of *Apriculus praeteritus* has been recovered during our work at Badwater. The species is known only from the type specimen. The other dichobunids present are represented by single teeth and cannot be assigned to genus.

Apriculus Gazin, 1956

Apriculus praeteritus

Holotype.—USNM 21100, RP⁴-M³.

Locality.—Probably locality 7.

Diagnosis.—Upper molars nearly quadrate with large lingually placed metaconule and simple conical cusps; no hypocone; no external styles; cingula continuous around molars; protoconule larger than in *Helohyus*.

Discussion.—Gazin (1956) provided an adequate description of the type and only known specimen. He suggested that *Apriculus* was descended from *Helohyus*. There are no known later descendants.



Figs. 2-4.—2) *Dichobunid* indet., CM 14552, RM^2 , $\times 3.5$. 3) *Dichobunid* indet., CM 19785, LM^3 , $\times 3$. 4) *Leptochoerid* indet., CM 16097, LM_2 , $\times 3.5$.

Dichobunids indet.

Figs. 2 and 3

Specimens.—CM 14552, RM^2 from locality 5 and CM 19785, LM^3 , from locality 7; USNM 20560, one half LM_3 , locality not known.

Description.—The M^2 is broken along the buccal border so that part of the paracone, the mesostyle, and the metacone/metastylar region are missing. The tooth has a greater transverse than anteroposterior width. The protocone is large and joins a distinct protoconule through a narrow crest. The protoconule in turn sends a crest into the parastyle. A large hypocone is present, isolated from both the protocone and metaconule. The latter is large. A short anterior cingulum is present below the protocone.

The M^3 is almost triangular in occlusal outline with the protocone situated at the interal apex. All cusps are rather high and sharp. There is a small parastyle and mesostyle but no metastyle. The protoconule and metaconule are large, sharp, and have both anterior and posterior crests. Those from the protoconule pass anteriorly to the parastyle and posteriorly to the base of the paracone; those from the metaconule are more isolated. The protocone and protoconule are connected about midway down the side of each cusp. Prominent anterior and posterior cingula are present, as is the stylar shelf. There is no hypocone.

Gazin (1956) referred a partial M_3 to *Pentacemylus*. The fragment is dichobunid but little more can be said about it.

Discussion.—The M^2 is somewhat reminiscent of that tooth in *Hylomeryx* and *Mytonomeryx* but one does not know whether a mesostyle was present, or not. The complete isolation of the hypocone clearly distinguishes the tooth as that of a dichobunid rather than a hypodont condylarth.

The M^3 is peculiar in possessing sharp cusps and a triangular shape. It resembles the M^3 of *Pentacemylus* somewhat, but the internal margin is much more acute than in that genus. The tooth might be an M^3 of *Auxontodon gazini* for which no upper dentition is known.

	Measurements	
	a-p	tr
CM 14552	6.25	—
CM 19785	5.86	8.20

Family LEPTOCHOERIDAE

Van Valen (1971) reduced the Leptochoeridae to a subfamily of the Dichobunidae saying only that, "They (Leptochoeridae and Dichobunidae) are sufficiently similar that familial separation seems unnecessary, so I reduce the Leptochoeridae to a subfamily (Leptochoerinae) of the Dichobunidae." I disagree and retain the family Leptochoeridae. The premolar dentition of *Stibarus*, *Leptochoerus*, and *Nanochoerus* is quite derived and differs markedly from that of any dichobunids. The pronounced reduction in the size of the molars from M^1_1 to M^3_3 also separates these families (Macdonald, 1955). Gazin (1955) suggested that the Leptochoeridae were possibly derived from *Diacodexis*, but he indicated that no intermediate forms were known between the Lost Cabinian *Diacodexis* and the first leptochoerid. The latter have not been previously reported from any Eocene fauna. The earliest known leptochoerids are the early Oligocene *Stibarus yoderensis* from the Yoder Formation of Wyoming and *Nanochoerus montanus* from Pipestone Springs, Montana (Macdonald, 1955). It is somewhat surprising that so little is known about the middle and late Eocene history of the family. West and Atkin (1970) have suggested that the Bridgeran *Neodiacodexis* may be related to the leptochoerids.

Stibarus is described as having paraconids on the lower molars, whereas *Nanochoerus* molars do not retain the paraconid. On this basis the single tooth described here is closer to *Stibarus* than to other Oligocene leptochoerids. It is smaller than any known Oligocene form. The single tooth from Badwater only serves to indicate that the family had differentiated by the late Eocene. Much more middle and late Eocene material will be needed to understand this origin.

Leptochoerid indet.

Fig. 4

Referred material.—CM 16079, LM₂.

Locality.—Wood locality.

Description.—The tooth is smaller than that of any other known leptochoerid, but it is morphologically almost indistinguishable from the M_2 of early Oligocene *Stibarus*. The trigonid is compressed anteroposteriorly with the paraconid still distinct as the tooth is unworn. With little wear the paraconid and metaconid would become one broad cusp. There is a distinct lophid from the protoconid to the metaconid. The trigonid basin is somewhat open posteriorly, more so than in the early Oligocene form. The protoconid and metaconid are of equal size with the hypoconid somewhat smaller and lower. There is a continuous anterior cingulum from the base of the parametaconid to the buccal face of the protoconid. The buccal valley is acute with the anterior crest from the hypoconid passing anterolingually into the protoconid-metaconid slope at the point where the trigonid basin opens posteriorly. A very small metastylid lies on the posterointernal face of the metaconid. The entoconid is broken away but was obviously separated from the metaconid by a deep notch. A small hypoconulid is present together with a narrow posterior cingulum.

Measurements

	a-p	tr
CM 16079	4.00	3.25

Discussion.—This single tooth appears to be unmistakably leptocherid in morphology. The paraconid is perhaps somewhat more distinct than in the Oligocene form and the principal cusps not as rounded and heavy. However, nothing can be said about leptocherid origins on the basis of a single tooth. It is of interest in indicating that the family had differentiated by the late Eocene.

Family AGRIOCHOERIDAE Leidy, 1869

In his paper on the Badwater fauna, Gazin (1956) recognized two large agriocherids, *Protoreodon pearcei* and *Diplobunops* cf. *D. matthewi*, together with two small protoreodont species, *Protoreodon* cf. *P. petersoni* and *P.* near *P. pumilus*. In the larger collection now available, I have been unable to distinguish *P. pumilus* from the large agriocherid present, which I consider to be *Diplobunops matthewi*.

Peterson (1919) originally described *Diplobunops matthewi* from Myton Pocket, Utah, based upon fragmentary skeletal, maxillary, and jaw material. He later described a second species *D. uintensis*, from northeast of Ouray, Utah (possibly what is now called Leota Bench), based upon a good skull. Gazin (1955) synonymized these two species and described a new form, *D. vanhouteni*, from the White River Pocket, Utah. A third species is also known, *D. crassus*, described by Scott (1945) from the Randlett Member of the Duchesne River Formation. This latter form, based on a nearly complete skull, is the largest known species of the genus.

In the Uinta Basin sequence *Diplobunops* is always the largest of the agriocherids present in any level and only a single lineage appears to be present. From its inception *Diplobunops* is distinguished from *Protoreodon* by characters of the rostrum and anterior premolar dentition. In other dental and postcranial characters the two genera are essentially identical. Although Gazin (1955) spoke of the less selenodont and somewhat more transverse molars in *Diplobunops*, there is too much variation in these rather subjective characters for their use as diagnostic features.

In the largest of the late Eocene agriocherids, there appears to be a great degree of what I interpret as sexual dimorphism. This is particularly evident in the Badwater sample, which consists of four good skulls, an additional snout, and many partial dentitions. In this sample, it is impossible to recognize more than one somewhat variable species based upon characters of the skull, jaw, and dentitions. However, there are two discrete morphologies for the snout, canines, and anterior premolars. Gazin recognized this state of affairs when he wrote

(1956:28–29), “The distinction between *Diplobunops* and *Protoreodon* on the basis of isolated teeth is difficult to make, particularly in the Badwater materials, because with the recognition of the equally large *Protoreodon pearcei* size is no longer an aid.”

Complete skulls in this sample do, however, display some differences. In USNM 20305, and CM 19726 and 19728 there is a diastema between the canine and P¹ and between P¹ and P². The snout in these skulls is elongate and broad and the canine large. This is very similar to the condition in a skull of *D. matthewi* from Uinta C, CM 11769. In the skull that Gazin made the type of *Protoreodon pearcei*, USNM 20305, the rostrum is slightly shorter (canine to posterior end of M³: 95 mm as opposed to 103 mm) than in CM 11769, the skull of *D. matthewi* and, while there is a canine to P¹ diastema, there is no P¹ to P² diastema (Gazin, 1956: Plate 3, Figs. 7–8). The canine in USNM 20305 is slightly smaller than in USNM 20303.

These rostral and dental differences in the Badwater sample are taken to reflect sexual dimorphism in a single population considered to represent *Diplobunops matthewi*. On all other skull and postcranial characters, the sample cannot be separated. Therefore, I am convinced that only one species of large agriochoerid is present in the Badwater fauna and that this form was conspecific with the Uinta Basin species. A smaller agriochoerid is also present in the Badwater fauna and is referred to *Protoreodon* cf. *P. petersoni*.

In California during the late Eocene, there is but a single species of *Protoreodon* present at any time (Golz, 1976:29, Fig. 7) beginning with *Protoreodon* cf. *P. parvus* in the Friars Formation, followed by *P. pumilus* in the Santiago and Sespe formations and finally by *P. pacificus* in the Pearson Ranch fauna of Duchesnean age. There is no large agriochoerid of *Diplobunops* size. This is in contrast to the diversity of *Protoreodon* species found in the intermontaine regions of Utah and Wyoming, and in Texas.

The greatest diversity of agriochoerid species is recorded from the late Eocene sequence in the Uinta Basin, Utah, where two species of *Diplobunops* and at least four and possibly five species of *Protoreodon* occur in the Uintan and Duchesnean intervals. In Texas two species of *Protoreodon* occur in the Candelaria fauna of Duchesnean age while one species of *Protoreodon* and one of *Agriochoerus* are present in the early Chadronian Porvenir fauna.

Diplobunops Peterson 1919

Diplobunops matthewi

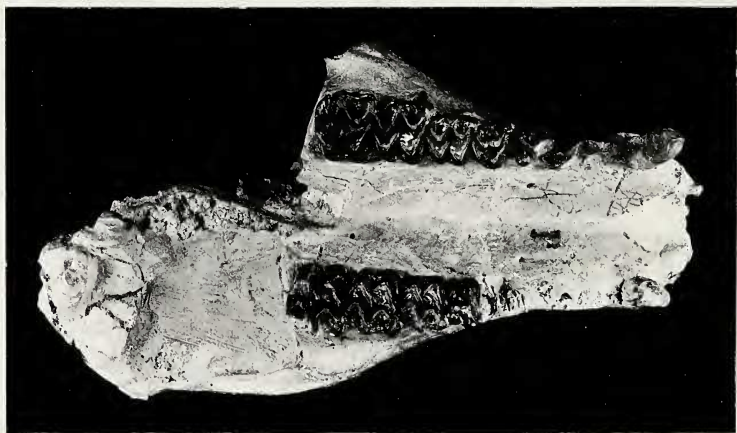
Figs. 5–11

Diplobunops matthewi Peterson 1919, pp. 62.

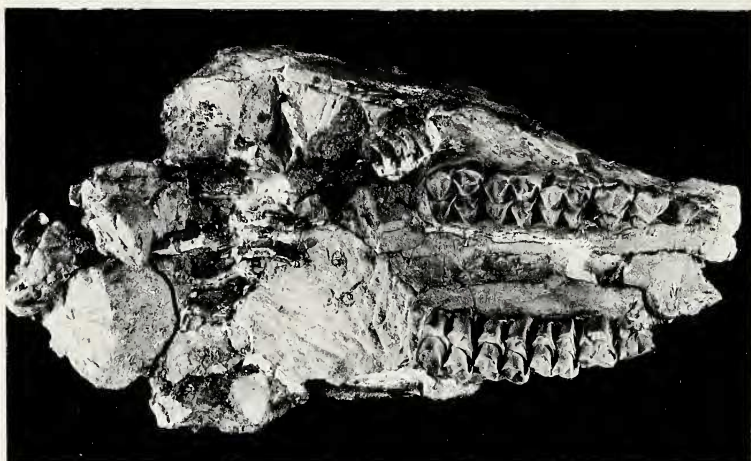
Protoreodon, near *P. pumilus* Gazin 1956, pp. 26.



5



6



7

Figs. 5-7.—*Diplobunops matthewi*, all $\times 1/2$. 5) Dorsal view of skull, USNM 20305. 6) Palatal view of same. 7) Palatal view of skull, CMNH 19728.

Protoreodon pearcei Gazin 1956, pp. 27.

Diplobunops cf. *matthewi* Gazin 1956, pp. 28.

Referred material.—USNM 20303 skulls and jaws, USNM, 20304, skull; CM 19728, skull; 17506, RP²-M³ and LP³-M³; 19726, R and LP²-P⁴; 14453, LdP³-dP⁴; 15751, LdP³-dP⁴-M¹; 19766, LM¹-M²; 17505, LM¹-M²; 17505, LM¹-M²; isolated upper teeth, 14450, 14477, 14537, 14544, 14590, 14595, 15387, 15333, 15752, 15755, 15931, 16059, 16777, 16780, 18252, 19556, 19730, 19733; 25334, RP₁-M₃; 19726, RP₁-P₄, M₂, LP₄-M₁; 19727, LP₃-M₃; 19729, R and LP₂-P₃; 14533, LP₂-P₃; 16055, RP₂-P₃; 19732, RP₃-dP₄; 15748, LP₃-dP₄-M₁; 14555, RdP₄-M₁; 16061, LdP₄-M₁; 14479, 29000, RP₄-M₁; 19765, RP₄-M₁; isolated lower teeth, 14434, 14435, 14439, 14467, 14551, 14552, 14586–14589, 14597, 15389, 15390, 15399, 15587, 15476, 15447, 15749, 15750, 15985, 16056, 16057, 16058, 16754, 16799, 17513, 17514, 17516, 21983, 21984, 21986.

Description.—Gazin (1955), Wilson (1971), and Golz (1976) have all given detailed descriptions of agriochoerid dentitions, which do not need to be repeated here for *Diplobunops matthewi*. The Badwater sample shows the P⁴ variation described by Wilson (1971:8–9) with some specimens having a partially divided parametacone while others show but a single cusp. On the molars the protoconule is generally present but becomes smaller from M¹ to M³. On one specimen (CM 17506) however, the protoconule appears to be absent on M³ and greatly reduced on M¹-M².

Sexual dimorphism is seen in the skull and jaws with some specimens displaying a short diastema between the upper canine and P¹ and between P¹ and P², whereas other specimens only have the canine-P¹ diastema. In the lower dentition some individuals have a P₁-P₂ diastema while in others there is no lower diastema at all.

In dental dimensions (Table 3) the Badwater sample of *Diplobunops matthewi* is no more variable than the Uinta Basin samples of *Protoreodon* measured by Wilson (1971: Tables 4–10). The coefficient of variation for most measurements lies between 4 and 9. All morphological and mensural data indicated that only a single, large agriochoerid is present in the Badwater fauna. Most of the specimens come from localities 5 and 6, with only three specimens known from locality 20 and two from the Wood locality.

Discussion.—Wilson (1971: Fig. 3) suggested that *Protoreodon pearcei* was ancestral to *Agriochoerus* and placed *Diplobunops* as a side lineage of Eocene agriochoerids without descendants. While synonymizing *P. pearcei* with *Diplobunops matthewi*, I still believe Wilson was most probably correct in deriving *Agriochoerus* from the large late Eocene agriochoerid complex. The reduction, and in some cases absence, of the protoconule on M¹-M³ in some of the Badwater specimens and the derived parametacone of P⁴ suggests this relationship.

Measurements of a-p length dentitions of *Diplobunops matthewi*
from Badwater

		C-M ³	P ¹ -M ³	P ¹ -P ⁴	M ¹ -M ³
USNM	20305	90.5	73.9	36.0	39.1
		95.6	—	—	40.0
CM	19728	—	—	—	41.1
		—	—	—	39.9
	19726	—	—	46.2	—
	17506	—	—	—	35.4
					35.4

		P ₁ -M ₃	P ₁ -P ₄	M ₁ -M ₃
USNM	20405	79.2	36.0	43.4
		82.0	38.0	43.5
CM	25334	88.8	43.3	45.6
	19726	—	43.2	—

Protoreodon Scott and Osborn, 1887

Protoreodon cf. *P. petersoni*

Referred material.—USNM 21101, RM¹-M³; CM 15977, LP²-dP³, 14525, 15413, 15414, 15754, 15757, 19731, isolated upper molars; 16055, RP₂-P₃.

Description.—There are only a few specimens of this small agriochoerid in the collections. As Gazin (1956:26) noted, the protoconule is weak on the upper molars. These specimens are all quite close to *P. petersoni* in size and are tentatively referred to that species.

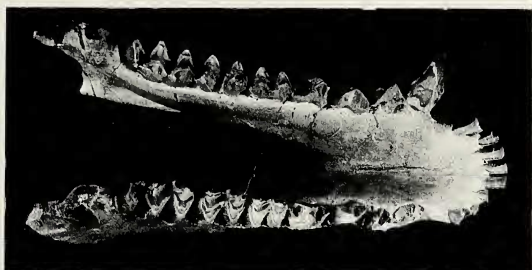
Measurements

	a-p	tr	a-p	tr
15977	P ² 7.1	4.0	dP ³ 8.5	6.7
14525	upper molar		6.0	6.8
15413	upper molar		6.8	7.8
15414	upper molar		7.0	7.6
15754	upper molar		8.4	9.8
19731	upper molar		8.3	10.8
15757	upper molar		8.6	11.9
16055	P ₂ 5.8	3.1	P ₃ 8.1	4.5

Family OROMERYCIDAE Gazin 1955

Gazin (1955:14 and 68) removed from the Camelidae the genera *Eotylopus*, *Camelodon*, *Protylopus*, and *Oromeryx* placing them in a new family, the Oromerycidae. At the same time, he described a new genus, *Malaquiferus*, assigning it to this family. This family was characterized as showing certain convergence to the camelids in the morphology of the lower premolars, the small canine and the procumbent lower incisors but in having strikingly different molar morphology. Also, all members of the Oromerycidae, as then known, were relatively short snouted forms with brachydont dentitions, not as slender limbed as the camelids and with separate metapodials.

Wilson (1974) disagreed with Gazin and reduced the Oromerycidae to a subfamily of the Camelidae, placing *Protylopus* as ancestral to *Poebrotherium*. Golz (1976:39–41) has recently thoroughly reviewed the taxonomic history of these genera and recognized the Oromerycidae as a distinct and possibly parallel group to the Camelidae. He suggests that *Poebrodon*, the earliest known camelid, may have



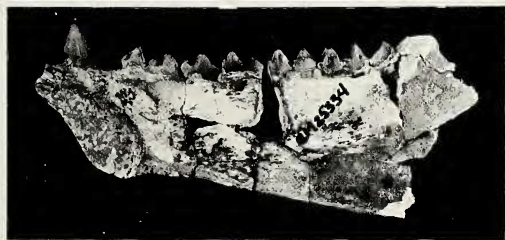
8



9



10



11

Figs. 8-11.—*Diplobunops matthewi*, all $\times 1/2$. 8) Dorsal view of mandible, USNM 20305. 9) Lateral view of same. 10) Dorsal view of right mandible, CMNH 25334. 11) Medial view of same.

Table 3.—*Statistical data on dentitions of Diplobunops matthewi from Badwater.*

Tooth and measurements	N	OR	M	SD	CV
P ¹ a-p	1		7.3	—	—
tr	1		4.3	—	—
P ² a-p	6	9.3–10.8	10.02	.496	4.95
tr	6	4.4– 6.2	5.6	.623	11.13
P ³ a-p	7	9.3–11.2	10.21	.727	7.12
tr	7	8.2–10.2	9.46	.787	8.32
P ⁴ a-p	11	7.1–10.9	9.67	1.18	12.20
tr	11	10.0–13.1	12.37	1.03	8.33
M ¹ a-p	9	10.3–12.3	11.39	.81	7.11
tr	10	12.0–15.0	13.70	1.21	8.83
M ² a-p	9	11.9–15.1	13.82	1.06	7.67
tr	9	14.2–18.1	16.49	1.49	9.04
M ³ a-p	6	13.3–15.5	14.50	.97	6.69
tr	7	15.7–18.6	17.71	1.32	7.45
dP ³ a-p	4	8.6–10.1	9.07	—	—
tr	4	6.7– 8.3	7.32	—	—
dP ⁴ a-p	3	9.0–11.5	10.00	—	—
tr	3	9.8–12.2	11.1	—	—
P ₁ a-p	3	8.4– 9.7	9.13	—	—
tr	3	6.1– 7.6	6.80	—	—
P ₂ a-p	9	7.8– 8.8	8.41	.407	4.84
tr	9	4.6– 5.1	4.73	.274	5.79
P ₃ a-p	15	8.1–10.5	10.7	.555	5.51
tr	15	4.5– 6.9	6.35	.479	7.54
P ₄ a-p	14	9.8–11.9	11.09	.635	6.00
tr	15	6.1– 8.8	7.54	.749	9.93
M ₁ a-p	19	9.1–12.0	10.69	.883	8.26
tr	19	7.2– 9.7	8.31	.758	9.12
M ₂ a-p	13	12.3–14.9	13.43	.865	6.44
tr	13	9.0–11.1	10.12	.608	6.01
M ₃ a-p	4	19.6–20.0	19.8	.231	1.17
tr	4	9.7–10.4	10.1	.294	0.40
dP ₄ a-p	5	11.5–13.0	12.24	.658	5.38
tr	5	6.0– 7.3	6.46	.522	8.08

evolved from a dichobunid line separate from that which gave rise to oromerycids. I agree with Golz that oromerycids do indeed appear to represent a distinct group of essentially late Eocene, partially selenodont, artiodactyls, which share certain characters with camelids (Fig. 1).

Although several oromerycids are known from the late Eocene of California and at least two, possibly three, from the earliest Oligocene of Texas, only one species of the family is recognized at present in the Badwater assemblages. *Malaquiferus tourteloti* is a specialized form, somewhat removed from the other members of the family. Its occurrence at Badwater is restricted to localities 5, 6, and 7 and Dry Creek, all of which produce a Uinta C equivalent fauna. *Malaquiferus* is not known from the younger Badwater faunas such as those from the Wood locality and locality 20.

Genus *Malaquiferus* Gazin, 1955

Type species.—*Malaquiferus tourteloti* (Gazin 1955:76).

Revised diagnosis.—Orbit large; snout short; cranium elongate; enamel of cheek teeth highly rugose; styles of upper molars weak, ribs strong; upper molars slightly oblique, approaching a square occlusal outline; small protoconule on M¹-M³; protocone only slightly bilobate; cheek teeth low crowned.

Type locality.—Section 11, T39N, R92W, 1½ mi northeast of East Fork of Dry Creek, Fremont County, Wyoming.

Age.—Uintan, late Eocene.

Distribution.—Only known from the type locality and from Badwater localities 5, 6, and 7.

Malaquiferus tourteloti Gazin 1955

Figs. 12–18

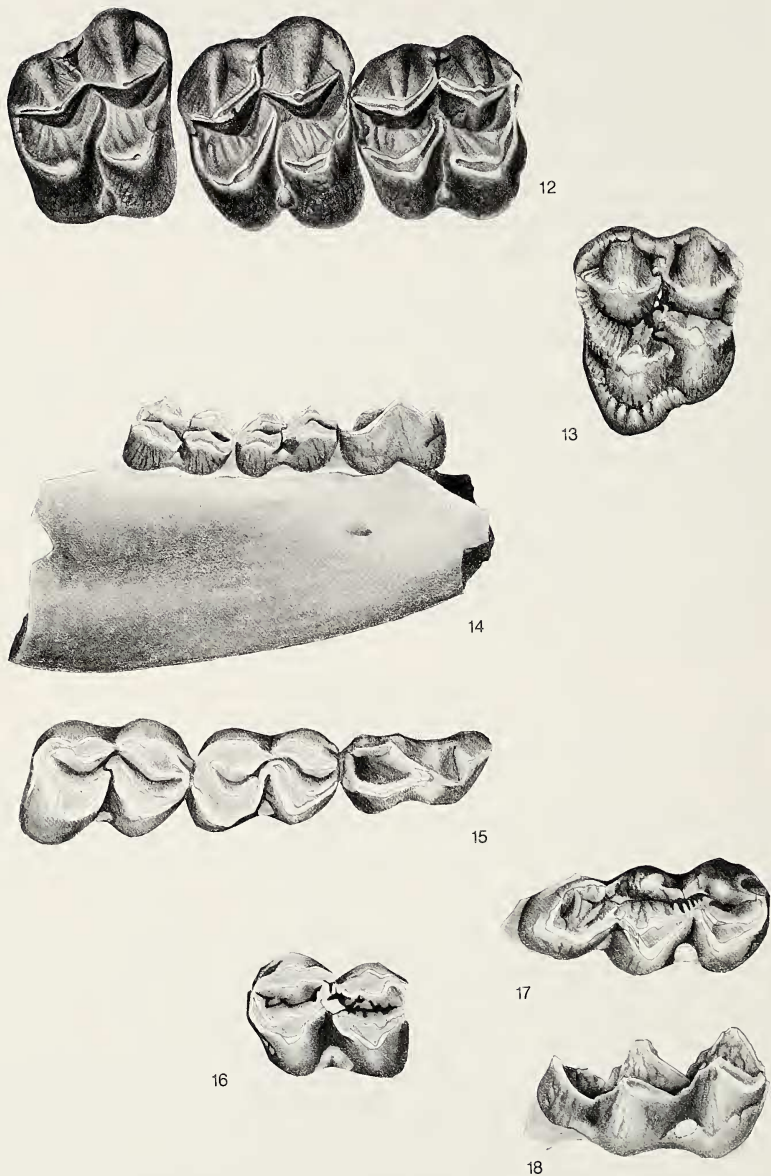
Holotype.—USNM 20588, greater part of a skull with R + LP⁴-M³.

Referred material.—CM 31395, LP³-P⁴; 15987, LP³; 15392, RM¹-M³; 14541, RM²-M³; 18248, RM²-M³; 14538, 14881, 15393, 15394, 15395, 15397, 15400, 15409, 15410, 13249, 18250, 19755, 19769, 29025, and USN, 21102, all isolated upper molars; 14438, RP₃-P₄; RP₄-M₂; 29497, LP₄-M₁; 15983, 18247, 25327, 29496, 14536, isolated lower M₁ and M₂; 15396, RM₃; 14433, LM₃.

Description.—The enamel on all the cheek teeth is quite wrinkled. The teeth are relatively low crowned and are bunoselenodont.

P₃ is elongate and rather narrow. The enamel is wrinkled. The parametacone is the only distinct cusp with both the parastyle and metastyle indistinct. There is a low ridge-like internal shelf with some swelling in the protocone position.

P⁴ is broader transversely than anteroposteriorly, more so than in *Protylopus* and *Eotylopus*. The tooth has three roots and is rather acutely triangular. The parastyle and metastyle are only moderately developed. The parametacone is undivided and bears a slight rib down its buccal face. The protocone is sharply conical and somewhat smaller than the parametacone. The cusps are more bunodont than those of *Protylopus* more as in *Merycobundon littoralis*. P⁴ is more anteroposteriorly compressed than in *Merycobundon*. The anterior crest from the protocone connects with the parastyle; the posterior crest is short, low, and quite wrinkled. It terminates below the posterointernal corner of the parametacone or the posterior cingulum. The posterior cingulum is long, while the anterior cingulum is restricted to a very small protruberance on the anterior face of the protocone.



Figs. 12-18.—*Malaquiferus tourteloti*. 12) CMNH 15392, RM¹-M³, ×3. 13) CMNH 14881, left upper molar, ×3. 14) CMNH 19737, RP₄-M₃, lateral view of mandible fragment, ×2. 15) Same occlusal view RP₄-M₂, ×3. 16) CMNH 18247, LM₁, ×3. 17-18) CMNH 15396, RM₃, ×3.

The upper molars are of approximately equal size, M^1 slightly smaller than M^2 and M^3 . The metacone on all is set somewhat internal to the paracones with the parastyles projecting buccally. However, particularly when worn, the molar occlusal outline is essentially square. The cusps are somewhat sharper than in *Merycobunodon* but not as selenodont as those of *Protylepus* and *Eotylepus*. There is some variation in the upper molars as to the degree in which the enamel is wrinkled. It is much more deeply wrinkled and pitted on the Badwater specimens than on the type (USNM 20588) from Dry Fork some 20 mi to the west.

The parastyle and mesostyle are prominent but low on M^1 - M^3 , whereas the paracone and metacone ribs are very strong on all molars. The metastyle is present on some teeth (CM 14551) and absent on others (CM 15392). The lingual cusps are moderately crescentic, whereas the labial ones are essentially conical with straight anteriorly and posteriorly directed crests, which form a nearly straight ectoloph.

A small protoconule (paraconule of Golz), situated on the anterior flank of the protocone somewhat below its apex, is also present on all upper molars. A short crest descends steeply from the protoconule to the parastyle. A posterior crest from the protocone is weakly but broadly bifurcate on all the upper molars. On all specimens there is a deep and quite narrow valley between the posterior protocone crest and the anterior crest of the metaconule, which drops steeply while passing labially to fuse with the reduced metastyle. A very short anterior cingulum is generally present on M^1 - M^3 but may be absent on M^3 (CM 15392). There is no strong internal cingulum as is seen on molars of *Merycobunodon* and to a lesser extent on *Protylepus*. A distinct cusp, quite low, is generally present filling the valley between the protocone and metaconule.

The lower dentition of *Malaquiferus* has not been previously described. The lower premolars and molars all have wrinkled enamel, although it is generally not as coarsely developed on the lower teeth as on the uppers, except perhaps on M^3 . The teeth are mesodont with the molar cusps bunoselenodont.

P_3 and P_4 are transversely compressed with the protoconid as the dominant cusp. There is a short crest from the protoconid to a strong triangularly shaped paraconid. Posteriorly a crest drops from the protoconid to the rear of the tooth, turns lingually and terminates at the posterointernal corner where it is joined by a crest from the metaconid. A rather deep and broad talonid basin is enclosed between the two crests. The metaconid is not distinct, but is represented by a slight swelling on the crest, which passes posterointernally from the protoconid. A short, narrow anterior cingulum is present well down the paraconid face.

M_1 and M_2 are subequal in size and show essentially the same morphology. The anterior and posterior moieties remain separate until the teeth are well worn. The principal cusps are of about equal size, although the metaconid and entoconid are somewhat higher and sharper cusps on unworn teeth (CM 19583). There is no indication of lingual stylids on M_1 - M_3 . The anterior crests from the protoconid and metaconid fuse early in wear giving a rather rounded occlusal appearance to the anterior face of M_1 and M_2 . The posterior crest from the protoconid passes internally but, rather than fusing with the crests of the lingual border, turns sharply back labially and fuses with the anterior arm of the hypoconid. There is thus a continuous shallow central valley between the labial and lingual cusps. Such is not the case in *Protylepus* and *Eotylepus*. The entoconid on M_1 and M_2 remains separate from the metaconid almost throughout the life of the molars. The entoconid and hypoconid join posteriorly through a broad, curving crest. The anterior cingulum on M_1 and M_2 is greatly reduced. There is a strong, low cusp between the protoconid and hypoconid filling the buccal valley.

The morphology of M_3 is essentially the same as that of M_1 and M_2 but with the addition of a complex third lobe posteriorly. The anterior cingulum on M_3 is strong and passes from the buccal border across the anterior face and around the lingual face of the metaconid. The protoconid-hypoconid crests join internally and send a short spur

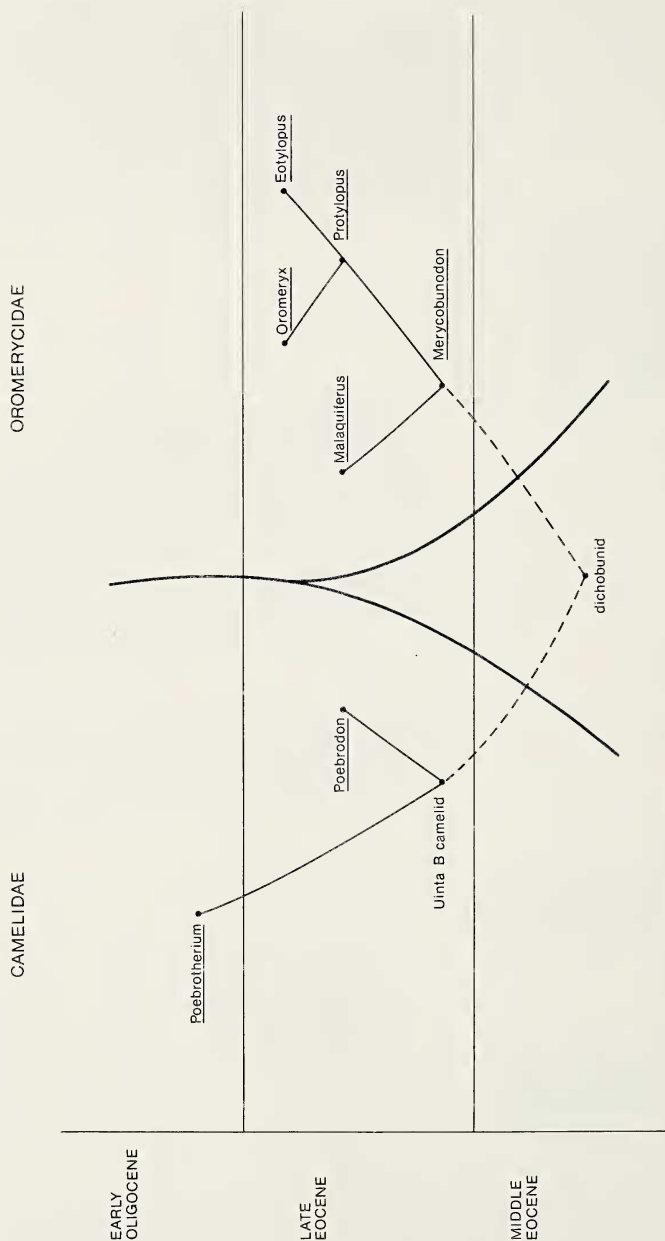


Fig. 19.—Suggested relationships of late Eocene Camelidae and Oromerycidae.

Table 4.—Statistical data on dentitions of *Malaquiferus tourteloti*.

Tooth and measurement	N	OR	M	SD	CV
P ⁴ a-p	1	5.8			
tr	1	6.5			
M ¹ a-p	4	6.1–6.8	6.45		
tr	4	6.8–7.8	7.40		
M ² a-p	10	7.0–7.8	7.45	.32	4.29
tr	10	7.9–9.4	7.73	.40	4.58
M ³ a-p	5	6.8–7.8	7.36	.48	6.52
tr	5	7.9–9.4	8.72	.55	6.32
P ₄ a-p	2	6.5–6.6	6.55		
tr	2	3.4–3.5	3.45		
M ₁ a-p	2	6.2–6.6	6.40		
tr	2	4.6	4.60		
M ₂ a-p	5	6.8–7.5	7.20	.33	4.58
tr	5	5.0–5.5	5.26	.19	3.61
M ₃ a-p	1	11.0			
tr	1	5.2			

into the posterior internal slope of the metaconid. The posterior hypoconid and entoconid crests pass directly posteriorly to form the complex posterior lobe. The basin of the posterior lobe is completely closed and is to a large extent filled and divided by a large central cusp. The lobe has a strong, distinct posteroexternal cusp and a smaller cusp at the rear of the entoconid.

A small portion of lower jaw is preserved (CM 19737), which shows that the mandible deepens from P₄ to M₃. A single mental foramina is preserved below the posterior half of P₄.

Discussion.—Golz (1976:39–41) provides a thorough review of the relationships of the members of the Oromerycidae. Of *Malaquiferus*, he says “*Malaquiferus tourteloti* of the Badwater fauna of Wyoming differs from other genera in relatively reduced styles and pronounced ribs on the upper molars. Its relationships to the other genera are not known.” On the basis of the much larger sample now available, I believe some suggestions as to its place in the family can be made.

Malaquiferus is primitive in the following characters: 1) displaying rather square and low crowned upper molars; 2) weak upper molar crests; 3) presence of protoconules on M¹–M³; 4) absence of stylids on lower molars; 5) weak crests on lower molars. The genus is specialized in the following characters: 6) the extreme wrinkling of the enamel of the cheek teeth; 7) prominence of ribs on M¹–M³; 8) absence of internal cingula on upper molars; 9) loss of hypocone; 10) bilobate posterior protocone crest; 11) subcrescentric metaconid and entoconid of M₁–M₃; absence of paraconid or parastylid; 12) some increase in crown height of lower molars.

In characters 1, 2, and 3, *Malaquiferus* resembles *Merycobunodon*, but it differs and appears more advanced in characters 6, 7, and 8. As no lower molars are known for *Merycobunodon* the two cannot be compared in other respects. *Malaquiferus* differs from *Protylopus* and *Oromeryx* in smaller size, having more nearly equal M¹ to M³, and in characters 1, 2, 5, 6, 7, and 8.

Malaquiferus would appear to be close to the dichobunid ancestry of the family in characters 1 through 5, but more advanced than the early Uinta *Merycobunodon* at least in the loss of internal cingula on the upper molars and in the degree of wrinkling of the enamel.

On this basis, I would suggest that *Malaquiferus* represents a relatively primitive oromerycid (Fig. 19) close to the point of origin of the family, possibly derived from *Merycobunodon*. Because of its highly wrinkled enamel and the loss of lingual upper molar cingula, I do not believe that *Malaquiferus* played any part in the ancestry of other oromerycid taxa.

Measurements in millimeters of teeth of *Malaquiferus tourteloti*

	P ₄		M ₁		M ₂		M ₃			
	a-p	tr	a-p	tr	a-p	tr	a-p	tr		
25327					6.9	5.2				
19737	6.5	3.5	6.2	4.6	6.8	5.4				
15396							11.0	5.2		
18247			6.6	4.6	7.5	5.5				
15983					7.5	5.2				
14536					7.3	5.0				
29497	6.6	3.4								
	P ³		P ⁴		M ¹		M ²		M ³	
15397							7.8	8.6		
18249							7.9	8.6		
18250							7.2	8.8		
18248							7.0	8.6	6.8	8.6
15395							7.3	8.8		
14538							7.2	8.5		
14541									7.8	8.7
14881							7.7	9.2		
29025									7.8	8.4
15395										
15392					6.5	7.2	7.2	7.9	6.9	7.9
19769					6.1	6.8				
19755							7.8	8.7		
19394					6.4	7.8				
31395	6.55	3.95	6.00	6.10						
USNM 20588			5.8	6.5	6.8	7.8	7.4	8.8	7.5	9.0

Family PROTOCERATIDAE Marsh, 1891

Subfamily LEPTOTRAGULINAE Zittel, 1893

Gazin (1955:17) placed three genera in the subfamily Leptotragulinae, two of which, *Leptotragulus* and *Leptoreodon*, are extremely difficult to differentiate one from the other. The third genus he included in this subfamily is *Poabromylus*. A fourth form, *Toromeryx*, recently described by Wilson (1974), should also be included here.

Leptotragulus is distinguished from *Leptoreodon* principally on characters of the lower premolars with almost no noticeable difference in the upper dentition or the lower M₁ to M₃ dentition. Likewise, the known skulls and postcranial material of the two genera are quite similar. Golz (1976:57) remarked on the great similarity of the two genera but refrained from synonymizing *Leptoreodon* with *Leptotragulus*, which has priority, having been described by Scott and Osborn in 1887. I, too, have retained both genera, although I believe that a thorough review of the now extensive collections referred to *Leptotragulus* and *Leptoreodon* would probably show them to be congeneric.

At present the two genera are separated on characters of P₃ and P₄; Gazin (1955:82) summarized these differences as follows: "In the lower jaws both P₃ and P₄ have an anterolingually directed crest from the protoconid, but in *Leptotragulus* the anterior extremity is more sharply flexed with a better-defined parastyloid. A posteroexternal crest extends from the protocone, then swings inward forming the posterior crest of the heel. A posterointernal crest extends posteriorly and only slightly inward from the apex of the protoconid but terminates before reaching the posterior crest, leaving the talonid basin broadly open lingually. In some material of *Leptotragulus*, this talonid basin of P₄ may be partially constricted medially by a slight implication from the posterointernal crest. In *Leptoreodon* there is a prominent metaconid posterointernal to the protoconid in P₄ and apparently also in P₃. Moreover, P₄ of *Leptoreodon* exhibits a usually distinctive, though variably developed, entoconid. In *Leptomeryx* the entoconid is well developed, and in P₄ joins the metaconid in early wear, but in P₃ joins the external crest well back of the protoconid."

In describing the California material, Golz (1976:57) noted some variation in these characters in specimens he assigned to species of *Leptoreodon*, although none of his examples of P₄ displayed either the weak metaconid or sharply flexed anterior crest of P₄ characteristic of *Leptotragulus*. In contrast most of the Badwater lower premolars show the *Leptotragulus* condition and only a relatively few have a large bulbous metaconid and the broadly flexed anterior crest on P₄.

Therefore, I have assigned the majority of the Badwater specimens to *Leptotragulus medius* while assigning only specimens displaying a

large metaconid on P_4 to the genus *Leptoreodon*. Two species of *Poa-bromylus* also occur in the Badwater faunas.

Leptotragulus Scott and Osborn, 1887

Leptotragulus medius Peterson, 1919

Figs. 20, 21, 23, 25

Material.—CM 19733, RdP⁴-M³; 15984, RdP³-dP⁴; 29014, LM¹-M³; 14592, 15974, P⁴; 14437, 14468, 14471, 14542, 14584, 15401, 15404, 15408, 15975, 16755, 16758, 16784, 16797, 18255, 19758, isolated upper molars; USNM 21103, RP₃-M₁; USNM 21104, LP₄-M₁; CM 31392, LP₃-M₃; 23974, LP₃-M₁; 29049, M₁-M₂; 14540, 14593, 15584, P₂; 14539, RdP₃; 14594, LdP₃; 16040, 16760, P₃; 29059, LdP₄; 16757, 16759, P₄; 14431, 14470, 15402, 15406, 15411, 15412, 15976, 15978-15980, 19759, 19771, 31394, isolated lower first or second molars; 15986, RM₃.

Description.—Much of the material consists of isolated teeth, although there are three maxillary fragments, which preserve deciduous upper molars and one almost complete jaw, CM 31392, from Dry Fork, which is badly broken and has quite worn molars. USNM 21103 and 21004 show the unworn P_4 together with M_1 .

The deciduous upper third molar is elongate and rather narrow, with the parastyle, paracone, and metacone strung out in a long anterior-posterior ridge. The protocone apex is set slightly in front of, and internal to, the metacone with short anterior and posterior lophs passing towards the metacone. The dP⁴ is slightly more transverse than elongate and is slightly skewed. The styles are prominent and the ribs reduced. This tooth is essentially molariform but considerably smaller than M¹. Permanent P⁴ is quite simple and triangular in occlusal outline. The parametacone is undivided and short crests pass from it to the low para- and metastyles. The protocone is sharply crescentic with low anterior and posterior crests passing to the styles. Short, internally restricted cingula are present.

The upper molars display essentially the same morphology and increase in size from M¹ to M³. They are somewhat transverse with the protocone on each set more lingually than the metaconule. The parastyles and mesostyles are more prominent than the metastyles on M¹-M³. Both paracone and metacone ribs are developed with the paracone rib the stronger of the two. The posterior crest from the paracone is short and does not fuse with the mesostyle until the tooth is well worn. The protocone and metaconule are sharply crescentic. The anterior arm of the protocone and the posterior arm of the metaconule pass to the internal side of the parastyle and metastyle. In the midline, the posterior arm of the protocone passes buccally between the paracone and metacone while the anterior crest from the metaconule is shorter and directed more into the base of the protocone crest. The anterior cingulum is strong but the lingual and posterior cingula are variable and usually only weakly developed. The lingual valley between the protocone and metaconule is shallow and constricted and there is no pillar at its internal margin.

The deciduous third and fourth lower premolars are longer than their permanent counterparts and taper anteriorly. There is no distinct paraconid on dP₃ and the anterior crest is short, with the protoconid set near the anterior end of the tooth. A crest passes diagonally from the posterolingual side of the protoconid to the posterobuccal corner where a large hypoconid is present. Two crests pass lingually from the hypoconid, one to a small entoconid, the other along the posterior border of the tooth. DP₄ bears six primary cusps and has a small anteriorly projecting cuspule in the middle of the anterior lophid.

P₂ is elongate and quite compressed laterally. There is a distinct paraconid set at an angle to the anterior crest from the protoconid. Two crests pass posteriorly from the protoconid to the posterior border and they enclose a narrow valley between them. P₃



20



21



22



23



24



25

Figs. 20–24.—*Leptotragulus* and *Leptoreodon*. 20) *Leptotragulus medius*, CMNH 19733, RdP⁴-M³, $\times 3$. 21) *Leptotragulus medius*, USNM 21103, RP₃-M₁, $\times 5$. 22) *Leptoreodon* sp., CMNH 29374, LP₄-M₁, $\times 5$. 23) *Leptotragulus medius*, CMNH 16040, RP₃, $\times 5$. 24) *Leptoreodon* sp., CMNH 21105, LP₄, $\times 5$.

Fig. 25.—*Leptotragulus medius*, CMNH 16757, $\times 5$.

and P₄ are somewhat broader than P₂ with more expanded talonids. On both, the paraconid is distinct and set at an angle to the anteroposterior axis of the tooth. A strong buccal crest passes from the protoconid posteriorly to the posterobuccal corner but no distinct entoconid is present. A much shorter crest passes from the protoconid posterolingually but this crest never reaches the posterior border. The talonid basin is open along the posterolingual margin of P₃ and P₄. No metaconid is present on either P₃ or P₄.

The lower molar cusps are quite sharp and high and the teeth increase in length from M_1 to M_3 . There is almost no trace of ribs on the metaconid and entoconid, and the parastylid is weak. The crests of the metaconid and entoconid are nearly straight but overlap slightly at the middle of the lingual margin. The median labial shelf is narrow and generally bears a small cuspule. The posterior arm of the hypoconid is strong and terminates behind the entoconid in a heavy ridge. The anterior and posterior cingula are moderately developed. M_3 has essentially the same structure as M_1 and M_2 with the addition of the third lobe. The basin of the posterior lobe is cut off from the basin between the hypoconid and entoconid by a strong crest.

Discussion.—This sample *Leptotragulus medius* is quite similar to that from the Uinta Basin. The divergent protoconid crests on P_3 and P_4 are particularly characteristic of this species (Gazin, 1955:85). A review of all material of both *Leptotragulus* and *Leptoreodon* is now needed to determine relationships in this subfamily.

Measurements of teeth of *Leptotragulus medius*

	dP ³		dP ⁴		M ¹		M ²		M ³	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 15984	6.15	4.00	5.35	5.65						
19733			5.40	5.65	5.90	7.05	6.40	8.30	7.10	8.60
29014					5.40	7.60	6.20	8.30	6.80	8.30
18208			5.30	—						
16758					6.00	6.80	6.80	8.35		
	P ³		P ⁴		isolated upper molars					
15987	6.45	4.25	5.90	6.80						
14592			5.10	6.30						
15974										
14437							6.50	8.60		
14438							6.60	8.50		
14542							7.00	8.40		
14584							6.60	8.50		
14685							7.10	8.90		
15401							7.90	8.65		
15404							6.85	9.10		
							a-p	tr		
15408							6.20	7.10		
15975							6.20	7.60		
16755							6.75	8.35		
16784							7.25	8.60		
16797							7.30	8.70		
18255							6.70	7.50		
19758							6.05	7.80		
	P ₂ -M ₃		P ₂ -P ₄		M ₁ -M ₃					
	a-p		a-p		a-p					
CM 31392	39.80		15.80		23.70					

	P ₃		P ₄		M ₁		M ₂		M ₃	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
31392	5.40	2.65	5.90	3.30	6.05	5.40	6.80	5.90	10.75	5.90
USNM 21103	5.50	2.60	6.10	3.45	6.75	5.10				
15986									9.95	5.75
	P ₂		P ₃		P ₄					
14540	5.10	1.90								
14593	5.20	2.30								
15584	5.20	1.90								
14438			5.75	3.00	6.05	3.50				
14539			6.00	3.30	deciduous					
14594			5.60	3.00	deciduous					
16760			6.20	2.90						
16757					5.75	2.85				
16759					6.15	2.90				
29059					7.30	3.60	deciduous			
							isolated lower molars			
							a-p	tr		
14431							7.30	5.40		
14470							6.05	4.50		
15402							6.60	5.20		
15406							7.10	5.65		
15411							5.90	4.95		
15412							5.90	4.60		
15976							6.45	5.10		
15978							6.80	5.60		
15979							6.35	5.20		
15980							6.60	5.15		
19759							6.95	5.30		
19771							7.40	5.10		
31394							6.60	5.20		

Leptoreodon Wortman, 1898

Leptoreodon sp.

Figs. 22, 24

Material.—USNM 21105, LP₄; CM 29374, LP₃-M₁; 14432, LP₄; 19734, RP₄.

Description.—The only specimens, which can be assigned to *Leptoreodon*, are those which preserve P₄. The lower M₁ in CM 29347 is indistinguishable from lower molars of *Leptotragulus medius*. The fourth lower premolars all have a robust metaconid and distinct ridge which runs from the metaconid to the rear of the tooth and which closes the talonid basin internally.

Measurements of teeth of *Leptoreodon* sp.

	P ₃		P ₄		M ₁	
	a-p	tr	a-p	tr	a-p	tr
CM 23974	5.60	2.45	5.90	3.60	6.60	5.10
14432			5.75	3.20		
19734			5.75	3.20		
21105			5.90	3.70		

Poabromylus Peterson 1931**Poabromylus golzi**, new species

Figs. 26-29

Holotype.—CM 25448, RP⁴-M³.*Hypodigm*.—Type and CM 29049, RP₂-P₃, M₁-M₂.*Locality*.—Badwater locality 20.

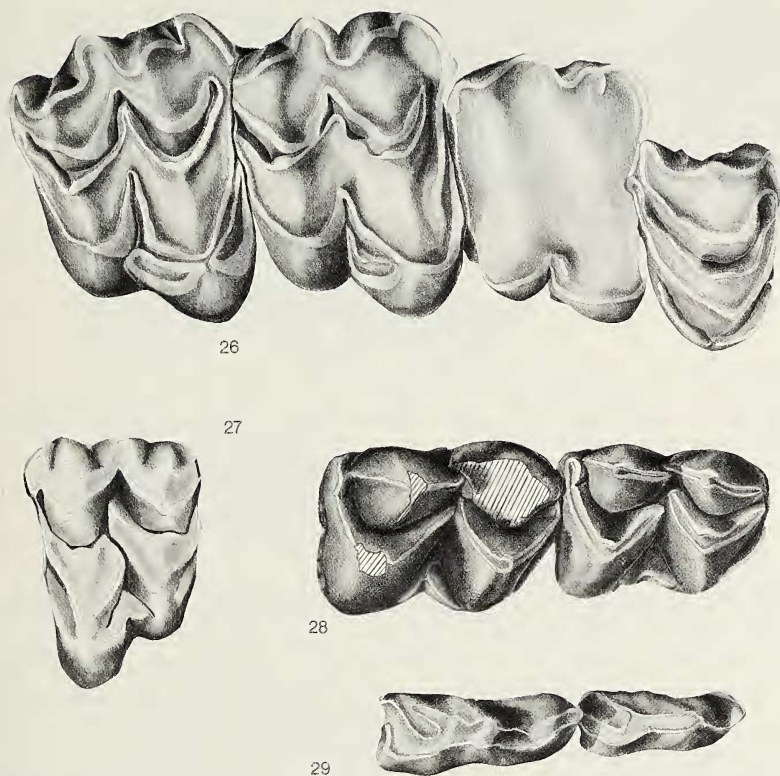
Diagnosis.—Smaller than *Poabromylus kayi*; cheek teeth lower crowned; enamel not as thick as in *Heteromeryx*; teeth higher crowned, more selenodont than in *Toromeryx*; internal cingulum complete on P⁴, reduced on M¹-M².

Etymology.—Named for David J. Golz who has recently reviewed the California late Eocene artiodactyls.

Description.—P⁴-M³ are distinctly wider than long, more pronouncedly so than in *Leptotragulus*. On P⁴ the parastyle and metastyle are strong and project buccally. The parametacone is undivided. The lingual cusp is V-shaped and sends crests buccally to fuse with the styles. A cingulum is complete on P⁴ from the anterior face around the inner cusp onto the posterior side of the tooth.

M¹ is so worn that all occlusal detail is obliterated. M² and M³ have strong anterobuccally projecting parastyles prominent mesostyles and on M³ a distinct mesostyle. The paracone and metacone are crescentic. The valleys between the paracone and protocone, and metacone and metaconule are fairly deep, more so than in *Heteromeryx*. The posterior crest from the protocone and the anterior crest from the metaconule pass buccally and fuse between the paracone and metacone. The anterior crest from the protocone passes externally to fuse with the parastyle and the posterior metaconule crest fuses with the metastyle on M³ while on M² it terminates at the posterointernal corner of the metacone. The anterior and posterior cingula on M¹-M³ are greatly reduced to absent; there is no buccal cingulum as in *Heteromeryx*. The internal cingulum between the protocone and metaconule is small.

In the lower dentition there is a diastema between P₁ and P₂ and from the shape of the alveolus P₁ was caniniform. P₂ and P₃ are elongate, narrow teeth, neither having a metaconid. From the protoconid a crest runs anteriorly to a distinct paraconid, which is set slightly to the internal side of the tooth. On both P₂ and P₃ the posterior crest from the protocone bifurcates, sending a narrow crest posterointernally and a stronger crest directly posteriorly to the end of the tooth. The internally directed crest does not reach the posterointernal corner of either P₂ and P₃. There is no distinct entoconid nor talonid basin. M₁ and M₂ are moderately high crowned with the labial cusps distinctly crescentic. The lingual cusps are sharp and the metaconid and entoconid are very short anterior and posterior crests and do not fuse into a lingual lophid until late in wear. The anterior crest from the protoconic terminates below the anterointernal corner



Figs. 26-29.—*Poabromylus golzi*. 26) CMNH 25448, RP^4-M^3 , $\times 3.5$. 27) CMNH 14474, LM^2 , $\times 3$. 28-29) CMNH 29049, RP_2P_3 , M_1-M_2 , $\times 3.5$.

of the metaconid; there is no stylid present. The posterior crest from the hypoconid passes to the lingual border terminating behind the entoconid. The anterior cingulum stretches across the entire anterior face of M_1 and M_2 . The external valley is deep and is filled at the buccal margin by a low pillar.

Measurements of teeth of *Poabromylus golzi*

	P^4		M^1		M^2		M^3	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 15248	5.60	7.25	7.20	9.25	8.10	10.75	8.50	10.55
CM 29049	P_2		P_3		M_1		M_2	
	5.90	2.30	7.00	2.85	7.50	5.45	8.10	6.30

Poabromylus cf. *P. golzi*

CM 14474					7.65	10.90		
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Discussion.—This species is referred to *Poabromylus* rather than *Leptoreodon* because of the absence of lower molar stylids, the even, broad crescentic selenes of M_1 - M_2 and the greater anterior transverse width than posterior in the upper molars. Also, the cingula of the upper molars are greatly reduced as they are in material referred to *Poabromylus kayi* by Wilson (1974: Fig. 13); upper molar cingula in *Poabromylus* are more reduced than in most *Leptoreodon* species.

Poabromylus golzi is smaller than *P. kayi* of the LaPoint. The latter is known only from a badly damaged lower jaw with P_3 to M_3 .

Poabromylus cf. P. golzi

Fig. 27

Referred material.—CM 14474, LM², from locality 7.

Description.—A single tooth from locality 7 is quite similar to the specimen from locality 20 but differs in having a much shorter posterior protocone crest and stronger anterior, posterior and internal cingula.

Family Leptomerycidae Scott, 1899

Hendryomeryx, new genus

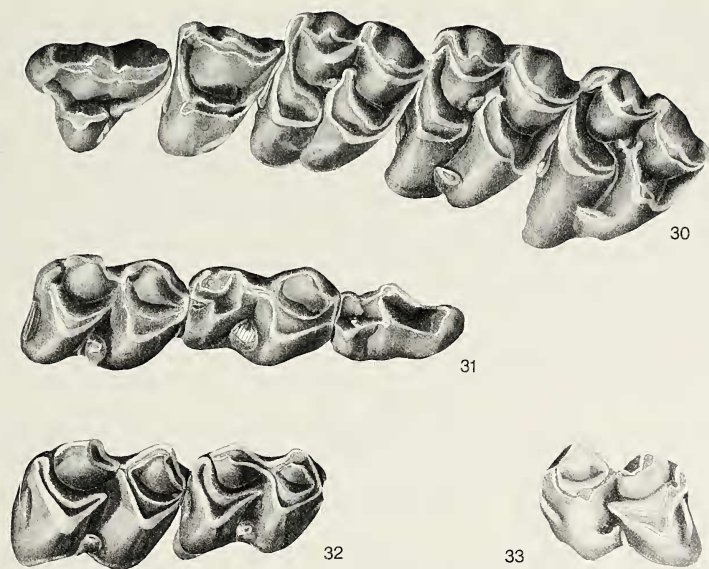
Type species.—*Hendryomeryx wilsoni*.

Generic diagnosis.—Protoconule absent on M^1 - M^3 ; all styles on M^1 - M^3 present but narrow; paracone rib developed on M^1 - M^3 , no metacone rib; posterior protocone crest very short, directed towards metaconule; P_4 talonid complex, enclosed; stylids on lower molars reduced or absent; selenes moderately developed on M_1 - M_3 ; entoconid and metaconid connected through a straight lingual crest.

Included species.—*Hendryomeryx wilsoni*; *Leptomeryx defordi* Wilson (1974:30); *Hendryomeryx* new species, unpublished from McCarty's Mountain, Montana (specimens in the Carnegie Museum collections).

Etymology.—Named for the Hendry family and the Greek *meryx*, ruminant.

Discussion.—*Hendryomeryx* is less advanced than the Oligocene *Leptomeryx* of the plains and intermontaine regions in having lower crowned, less selenodont molars, and a weak metaconid-entoconid lophid. *Hendryomeryx* is distinct from *Simimeryx* in the absence of the protoconule, presence of a mesostyle, in being somewhat more selenodont and in having more complex lower premolars. It has been suggested (Stock, 1934; Gazin, 1955; Golz, 1976) that *Simimeryx hudsoni* may be ancestral to *Hypertragulus* and that *Leptomeryx* be included with them in the family Hypertragulidae (Wilson, 1973). The lower premolars of *Simimeryx* are quite simple, much more so than in any of the *Hendryomeryx* species. In this respect *Simimeryx* is much closer to *Hypertragulus* than to *Hendryomeryx* and *Leptomeryx* and the latter two genera are hence placed in the Leptomerycidae.



Figs. 30–33.—*Hendryomeryx wilsoni*. 30) CMNH 29120, LP³-M³, ×3.5. 31) CMNH 29013, RP₄-M₂, ×3.5. 32) CMNH 29050, RM₁-M₂, ×3.5. 33) CMNH 18258, ×4.

Hendryomeryx wilsoni new species

Figs. 30–32

Holotype.—CM 29102, LP³-M³.

Hypodigm.—Type and CM 31391, RdP⁴-M¹, 31393, LdP⁴-M¹; 29056, RP²; 29054 RdP³ 29023, 29060, P³; 29013, RP₄-M₂; 29050, RM₁-M₂; 29044, LP₂; 29035, RM₁.

Locality.—All from Badwater locality 20.

Diagnosis.—Smaller, less high crowned molars than *Hendryomeryx defordi*; lower molars not as selenodont as in that species.

Etymology.—Named for John A. Wilson who has done extensive work on the Texas Eocene and Oligocene artiodactyls.

Description.—The type maxilla (CM 29120) shows slight wear on P³-P⁴, moderately worn M¹ and light wear on M²-M³. No P² is associated with the type, but an isolated P² (CM 29056) is assigned to the species. P² is three rooted but there is no internal median cusp. The paracone is sharp and sends crests directly anteriorly to a large parastyle and directly posteriorly to the end of the tooth. No metacone or metastyle is present. A narrow internal cingulum runs from below the paracone posteriorly to the rear of P². There are shallow concavities on the buccal face of P² before and behind the paracone.

P³ on the type has the paracone and parastyle set close together. There is a slight indication of a metacone behind the paracone, but it is not large, and the posterior crest from the paracone passes through it to the posteroexternal corner of the tooth. The internal cusp is quite large on P³ and connects to both the parastyle and the posteroexternal corner through low, thin ridges.

On P^4 the paracone is high and sharp with no indication of a metacone. The parastyle is quite small and low and there is no distinct metastyle. The internal cusp is crescentic with low but prominent anterior and posterior crests which pass to the parastyle and the posterorexternal corner. Very short narrow anterior and posterior cingula are present on P^4 near the internal base of the internal cusp.

The upper molars are essentially identical in structure, with M^1 somewhat smaller than M^2 and M^3 . On all molars the parastyle and mesostyle are compressed but distinct and the metastyle while present is smaller. There is a prominent rib on the paracone on M^1 - M^3 , but no distinct metacone rib. The anterior crest from the protocone terminates at the parastyle and carries a short, narrow anterior cingulum below the apex of the protocone. The posterior arm of the protocone is indistinct with the posterointernal face sloping off towards the metaconule. A deep, narrow valley separates the protocone from the metaconule and anterior crest of the metaconule. The latter passes buccally to terminate between the paracone and metacone. There is a distinct small pillar between the interior face of the paracone and the end of the anterior crest from the metaconule which, with wear, fuses with the crest forming a spur into the slope of the paracone. The posterior crest from the metaconule passes buccally to terminate at the posterointernal base of the metacone. There is no posterior cingulum on M^1 - M^3 . On all M^1 of CM 31391 there is a very faint suggestion of a remnant of the protoconule given by a shallow groove down the internal face of the anterior crest of the protocone also on this specimen dP^4 is preserved. The tooth is essentially molariform displaying, on a smaller scale, the same features seen on M^1 .

P_2 is elongate and quite narrow. It is rather complex with a distinct protoconid and metaconid the latter lying directly internal to the protoconid. The paraconid is large and the protoconid crest to the paraconid bends sharply internally. There is no posterior crest from the metaconid and hence no enclosed talonid basin. A crest passes directly posteriorly from the protoconid to the rear of the tooth. There is no distinct entoconid.

P_3 is not known. P_4 is quite complex with the protoconid and metaconid of equal size. An anterior crest descends steeply to the low parastylid which is set at a sharp angle to the crest. Posterior crests pass buccally from the protoconid to a distinct hypoconid and from the metaconid to a distinct entoconid. There crests enclose a narrow, deep talonid basin which is closed posteriorly by a high hypoconid-entoconid crest. A very narrow, short cingulum is present on the buccal face below and behind the parastylid.

M_1 and M_2 are rather low crowned, more so than in *Hendryomeryx defordi*. The metaconid and entoconid are sharp and project above the protoconid and hypoconid. There are no stylids on M_1 or M_2 . The anterior crest of the entoconid fuses with the posterior crest of the protoconid. The anterior crest of the hypoconid passes anterointernally to merge into the lower slope of the posterior protoconid crest. The posterior crest of the entoconid terminates at the posterointernal corner of M_1 and M_2 . No anterior cingulum is present on M_1 , but a very short narrow cingulum is present on both M_1 and M_2 . The buccal valley is closed by a low pillar on both M_1 and M_2 . In CM 29013 M_1 is somewhat aberrant with the hypoconid and entoconid essentially fused with a V-shaped valley between them.

Discussion.—*Hendryomeryx wilsoni* is quite distinct from any of the other selenodont artiodactyls in the Badwater faunas. It closely resembles *Hendryomeryx defordi* (Wilson) from the Porvenir fauna of west Texas. The latter is somewhat larger and slightly higher crowned than *H. wilsoni*. In the McCarty's Mountain fauna in Montana an undescribed species of *Hendryomeryx* appears to be present (CM 1057 and 31397) together with a species of *Leptomeryx*. The latter is higher

crowned, larger, and more selenodont. The early Oligocene leptomerycines need to be thoroughly restudied, but it appears likely that they evolved from *Hendryomeryx*. *Hendryomeryx defordi* (Wilson) from the Porvenir fauna of Texas is somewhat larger and slightly higher crowned than *H. wilsoni* and may well have evolved from that species.

The origin of *Hendryomeryx* within the dichobunids is unclear. No known early Uintan or late Bridgerian form appears at present to be a more likely ancestor than any other.

Hendryomeryx cf. H. wilsoni

Fig. 33

Material.—CM 29499, RM¹; 29498, RM²; 18025, RM₁; 16021, RM₁ or ₂; 18258, LM₁ or ₂.

Locality.—Wood and Rodent localities.

Description.—These specimens are all quite similar to material described for *Hendryomeryx wilsoni*. The lower molars are somewhat lower crowned with the hypoconid selene perhaps less crescentic. In other features they are essentially identical to the specimens from locality 20.

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